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US ARMY MEDICAL RESEARCH LABORATORY

FORT KNOX, KENTUCKY

REPORT NO. 488

HABITUATION OF VESTIBULAR NYSTAGMUS IN THE CAT DURING SUSTAINED AROUSAL PRODUCED BY d-AMPHETAMINE

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Vestibular Function and Acceleration in Relation to Performance
Task 04
Psychophysiological Studies
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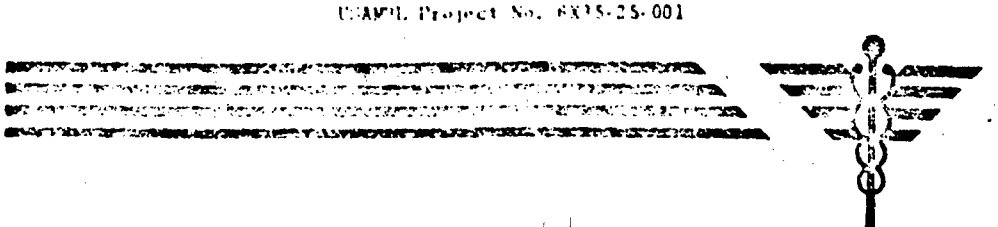

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ABSTRACT

HABITUATION OF VESTIBULAR NYSTAGMUS IN THE CAT DURING SUSTAINED AROUSAL PRODUCED BY d-AMPHETAMINE

OBJECT

These observations were designed to determine if habituation of ocular nystagmus in total darkness would occur when cats were maintained in a continuous state of arousal with d-amphetamine sulfate.

RESULTS

Amphetamine served to increase nystagmic output of the drug group by nearly 60 per cent over that of the control group, but the drug group showed a habituation that was equal in magnitude to that of the control group.

CONCLUSIONS

A loss of nystagmic output does occur in cat that cannot be attributed simply to a loss of generalized arousal. Other factors must be of importance to the habituation process. Two factors that have been proposed, a) learning, and b) fatigue of sensory and neural structures, are discussed.

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I. INTRODUCTION

Nystagmus is reduced by repeatedly rotating an animal. This reduction of the response has been termed "habituation" (1), and is a common finding for all birds and mammals that have been studied.

Alertness is one important factor that determines the magnitude of the ocular nystagmic reaction (3, 5, 6, 22), and habituation has been attributed entirely to a reduction of alertness (28). In a previous experiment from this laboratory (7) it was determined for cat that the arousal reaction precipitated only a partial and temporary recovery of nystagmic output. Further, nystagmus still habituated under conditions in which arousal was maintained by frequent cutaneous electric shocks, and it was concluded that arousal was only one of several variables responsible for the reduction of nystagmus.

It was found that the alerting shocks had to be administered at a greater frequency and at increasing intensity levels in order to insure a flat, desynchronized electroencephalographic (EEG) pattern. In other words, the cat habituated to the shocks as well, a phenomenon that has been intensively studied with auditory stimuli (25). This habituation to the shocks was a shortcoming of the earlier experiment, since the maintenance of the arousal depended upon the astuteness of the experimenter in assessing the EEG and appropriately manipulating the stimulating shocks.

The present experiment is intended to complement the earlier results by controlling arousal with a drug.[1] It has been shown (4) that a cat is easily alerted both behaviorially and electrically after a dose of 1 mg/kg body weight of d-amphetamine, and as the dosage is increased, a continuous arousal is manifested. This drug promised to be of great value in maintaining a continuous arousal without the complications of habituation to auxiliary alerting stimuli as in the previous experiment. In this experiment, a group of animals received d-amphetamine injections and was compared to a group of untreated control animals on an identical series of angular accelerations. All testing was performed in total darkness.

[1] The author is indebted to Dr. Seth Sharpless, Albert Einstein College of Medicine, for suggesting this method of controlling arousal, and to Captain Wayne O. Evans, US Army Medical Research Laboratory, for advise on establishing the dosage and on other critical details.

II. METHOD

Apparatus. The turntable was 2.4 meters in diameter and was equipped with suitable feedback circuitry to maintain the required acceleration programs (13). The cats were restrained by a method developed by Dr. Cesar Fernandez of the University of Chicago (17). Under Nembutal anesthesia, a small hole was drilled in each canine tooth (Fig. 1). Several days later, and just prior to testing, the cat was wrapped snuggly in cloth and fitted into a rabbit box. Number 8 music wire (piano wire) was then strung through the holes and drawn to a high tension in the special vise arrangement shown in the figure. This technique assures that the head will be firmly fixed, a necessary procedure to prevent intrusion of the disturbing Coriolis phenomena (14).

It should be added that this method is far superior to the casting technique described earlier (8), in that it fits all cats easily and with little preparation. The teeth rarely break, do not decay, and most important, the cat shows no discomfort. Cats, in the holder, sometimes sleep if undisturbed.

Each cat was mounted on the turntable with the head over the axis of rotation in a light-proof, ventilated and electrically shielded enclosure that has been used in previous studies (7). Needle electrodes were inserted at the outer canthi to record eye-movements by the electro-oculo-graphic (EOG) technique (21). An additional pair of electrodes was inserted in skin on the crown, straddling the midline, to monitor the EEG. The ground connection was made to the wire strung through the teeth. EOG potentials were amplified with a 1.4 sec RC time constant and all potentials recorded on an Offner type T ink-writing electroencephalograph.

Subjects. The control and drug groups consisted of ten mature cats each.

Procedure. The two groups were identically treated except that each animal in the drug group received an interperitoneal injection of d-amphetamine sulfate (3 mg/kg body weight) in saline solution 60 to 90 minutes prior to the first trial.

The testing procedure started with a period of 10 min in which the cat was maintained quietly in total darkness. The turntable was then set at a clockwise base speed of 1 RPM by means of a brief and subthreshold acceleration. A series of acceleration trials followed. A trial commenced with a 4.5°/sec^2 acceleration of 14.9 sec duration followed by a 10 sec period of constant velocity. The turntable was then decelerated to the base speed of 1 RPM with a subthreshold deceleration

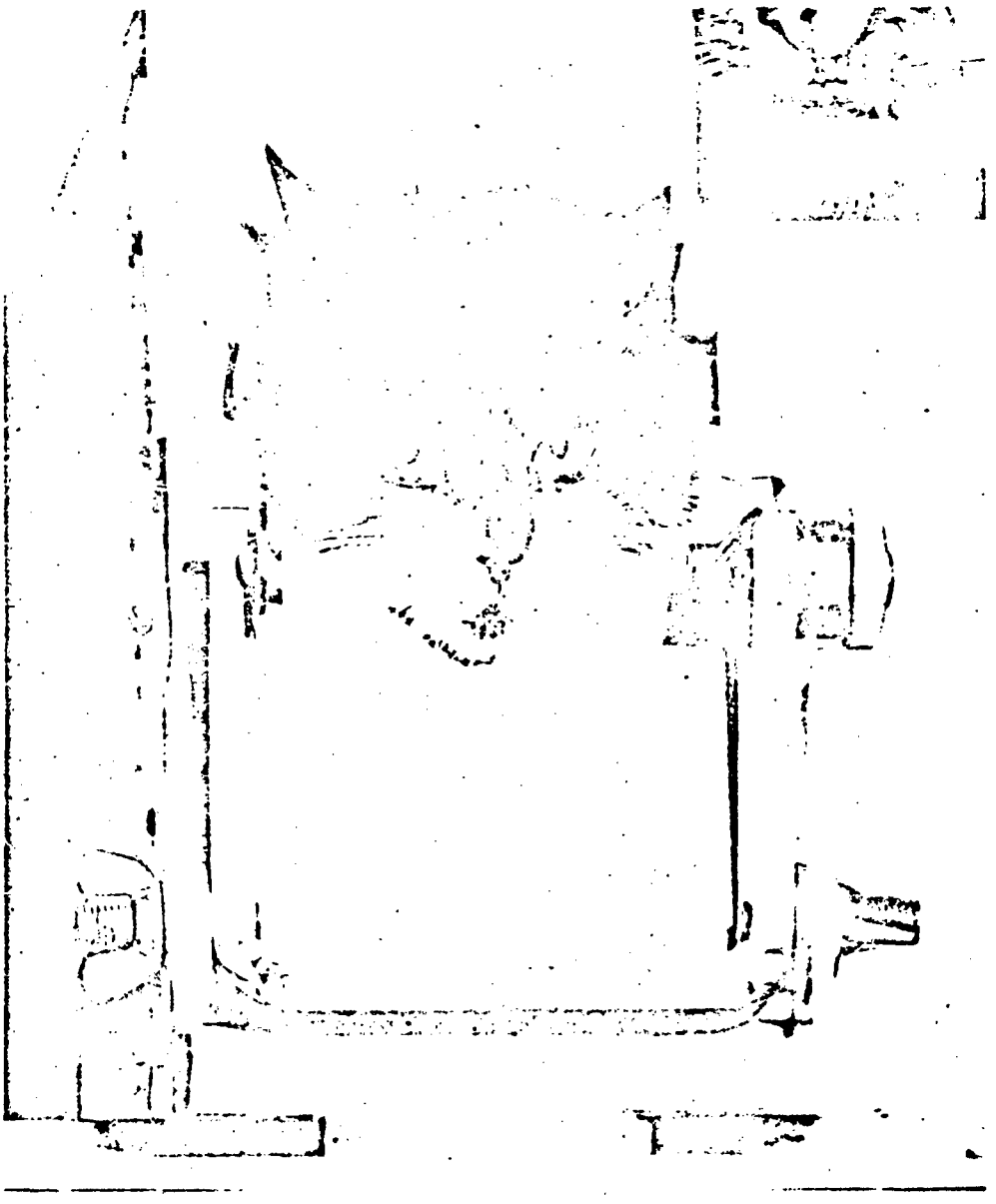

Fig. 1. Restraint method developed by Henriksson, Fernandez and Kohut (17). Several days prior to testing, holes were drilled through the canine teeth while the animal was suitably anesthetized. Just prior to testing, the wire was passed through the holes and drawn taut in this vise arrangement. In the insert, a gentle retraction of the lip reveals the wire and tooth detail.

of .28°/sec^2. The deceleration required 4 min, 3 sec. Shortly after the 1 RPM base speed was attained, the succeeding trial was commenced. Acceleration trials were therefore spaced at 4 to 5 min intervals. Each cat received a series of 12 trials and was maintained in total darkness throughout the testing period.

The EEG was monitored for all cats. The animals with d-amphetamine always displayed a fast low voltage EEG containing a great deal of muscle activity. The control animals, on the other hand, would show some slower activity if they were left undisturbed. The experimenter alerted a control cat by knocking sharply on the metal enclosure whenever the EEG indicated slow wave activity.

III. RESULTS

In Figure 2 are typical examples of nystagmus from a control animal and from one under the influence of d-amphetamine. The examples are from the 12th and final trial of the experiment. Quantitatively there are more nystagmic beats and a much longer duration for the d-amphetamine animal; qualitatively, the drug animal also shows sharper or "crisper" beats than does the control animal.

The recordings were treated as in an earlier paper (7). The slow-phase excursions for the entire period of the primary nystagmus were cumulated and converted into millivolts for each cat for each trial. The secondary nystagmus was not scored.

In Figure 3, page 6, the averages of the two groups of animals are plotted. The individual data from all animals may be found in the Appendix. The d-amphetamine group always showed substantially more nystagmic output than the control group throughout the series of trials.

Table 1, page 7, summarizes the variance analysis of the graphed data in Figure 3. The analysis follows that described by Edwards (10) for use with repeated measures of the same subjects. The test for significance between the two methods (control vs. drug groups) employs the mean square between cats in the same group as the error term. The difference between the groups was found to be significant at the .05 level. The pooled cats x trials interaction mean square was the error term for testing the between trials variance and the trials x methods interaction. It was clearly shown that the trials do result in a significant difference at the .001 level. The trials x methods interaction was not significant.

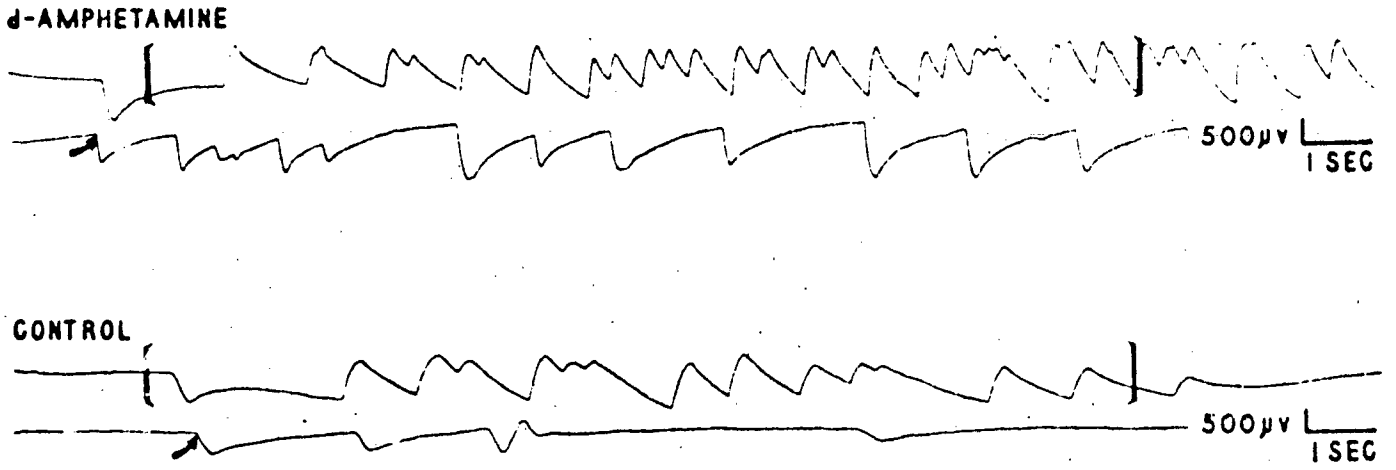

Fig. 2. Examples of rystagmus on the 12th and final trial of the habituation series for a control animal and one receiving a 3 mg/kg interperitoneal injection of d-amphetamine sulfate. The brackets mark off the period of acceleration and the arrows indicate the onset of the secondary nystagmus. The secondary nystagmus continued for 5 sec longer than is included in this d-amphetamine example.

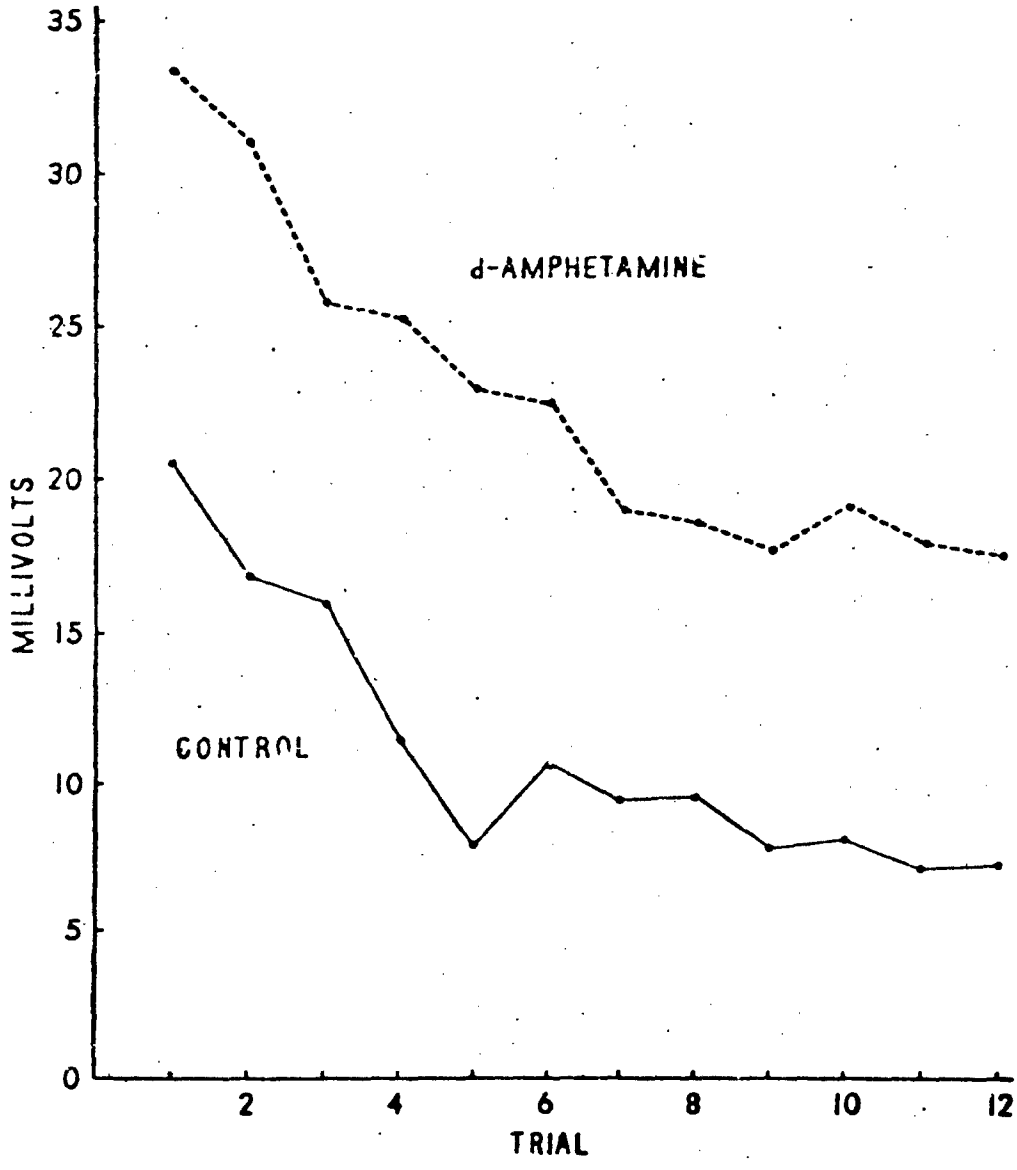

Fig. 3. Slow-phase activity of primary nystagmus in millivolts for a series of 12 trials. Each point represents the average of 10 animals. A trial consisted of a 4.5°/sec^2 acceleration of 14.9 sec duration followed by a long period of subthreshold deceleration. Accelerations were spaced at 4 to 5 min intervals.

TABLE 1

VARIANCE ANALYSIS OF DATA GRAPHED IN FIGURE 3

Source of Variation	Sum of Squares	df	Mean Square	F
Between methods: drug vs. control	8,045.78	1	8,045.78	13.95*
Between cats in same group	10,384.35	18	576.91	
Total between cats	18,430.13	19		
Between trials: 1-12	5,055.96	11	459.63	20.68**
Interaction: trials x methods	220.76	11	20.07	- -
Interaction: pooled cats x trials	4,400.62	198	22.22	
Total within cats	9,677.34	220		
Total	28,107.47	239		

* .05 level of significance
** .001 level of significance

IV. DISCUSSION

The most significant aspect of these data is that the animals which were maintained in sustained arousal showed a decrement in response with repeated testing. This is in agreement with the data of a previous experiment (7) in which sensory methods of arousal control were employed. Clearly, nystagmic output is dependent only in part upon arousal level, and a reduction of the latter does not along account for all of the vestibular response decrement obtained by repeated tests.

The arousal variable is of a generalized nature. An alerting or attention which is specific to the vestibular stimulus is not required. The earlier experiment with cat (7) showed that either auditory stimuli or cutaneous electric shocks would serve to increase nystagmic output. Further, experiments with man have clearly demonstrated that the variable may be defined in terms of degree of mental effort. Continuous, silent mental arithmetic has been shown to be more efficacious in producing a nystagmic response than attending to rotary sensations and signalling subjective events (5). Parenthetically, electroencephalographic correlates of mental effort and nystagmic output were not found in man (6).

This experiment does not definitely demonstrate that d-amphetamine acts only by virtue of assuring a continuous desynchronized EEG and a behavioral arousal. This drug may have other and perhaps specific effects on vestibular function. Further work with other stimulants is needed.

The conclusion appears to hold that alerting or arousal is only responsible for part of the loss of nystagmus with repeated testing. Other factors must be of importance. Prominent among the proposed hypotheses is that which invokes a fatigue or at least some change in those nerve cells associated with vestibular function. Hamberger and Hydén (15, 16) have determined increases in nucleoproteins in the vestibular ganglion and Deiters' nucleus following moderate treatments of angular accelerations of the rabbit. Although the distribution of changes is appropriate, their short time course (48 hr) does not correlate well with the long duration characteristic of habituation. There is, as yet, no clear evidence for a fatigue explanation and further work is required with sophisticated and well-controlled vestibular experiments. In particular, it would be of importance to determine if these changes would occur in anesthetized animals in which habituation is known not to occur (11, 18).

There is a third hypotheses for habituation of nystagmus which implicates a learning or functional alteration. When vision is permitted during rotation there is a systematic decline of nystagmus with each stimulation. Dodge (9) and Wendt (27) have examined this decline in detail and have characterized the loss of vestibular nystagmus as the resolution of the conflict between competing visual and vestibular inputs, in which the visual input gains ascendency in determining the spatial orientation. A loss of nystagmic output with training for certain occupations is a common finding; for example in pilots (2), and skaters (20).

Thorpe (26) has described habituation as a specific form of learning in which the intensity of a reflex is reduced if the reflex is repeatedly elicited but not followed by some significant consequence for the organism. Hood and Pfaltz (18) have likened nystagmus habituation to this type of learning. Of special relevance to nystagmus habituation is that a competition between sensory inputs is not a requirement. There is some evidence from electrophysiology indicating the possible neural correlates underlying this form of habituation. In particular, an evoked potential also declines in amplitude if elicited over many occasions in which the evoking stimulus is not paired with an unconditioned stimulus (see recent review by John, 19). The precise neural mechanisms that might underlie vestibular habituation are a matter for speculation. Perhaps the vestibular efferents (23, 24) play a role similar to that implicated for the auditory efferents in audition (12).

V. SUMMARY

The habituation of nystagmus in total darkness was examined for two groups of cats. One group was maintained in a continuous arousal with d-amphetamine sulfate and compared to the second group of

untreated controls. The drug group displayed nystagmus of nearly 60 per cent greater output than the controls but showed the same magnitude of habituation. The data of this experiment confirm the earlier observations. A reduction of arousal is only one variable responsible for a reduction of nystagmus with repeated testing, and nystagmus still habituates even when a high level of arousal is maintained. Other possible responsible factors are discussed.

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APPENDIX

TABLE 2

NYSTAGMIC OUTPUT IN MILLIVOLTS FOR EACH TRIAL AND EACH CAT IN THE d-AMPHETAMINE GROUP

Cat Number	TRIAL 1	2	3	4	5	6	7	8	9	10	11	12
84	12.7	13.3	11.3	14.6	4.1	14.9	6.2	14.9	13.1	8.1	7.8	8.3
85	11.3	26.1	13.9	8.6	21.9	14.8	2.6	15.1	6.6	12.8	11.9	10.4
87	52.6	46.0	18.6	41.7	39.8	34.6	33.2	25.2	28.2	27.0	27.7	33.9
90	36.7	32.1	27.4	23.5	23.3	30.4	34.0	24.2	19.2	30.8	25.7	27.4
92	48.1	46.6	38.2	37.6	32.1	27.2	22.5	21.2	22.7	25.6	24.1	22.0
95	19.9	14.1	9.0	12.7	14.9	13.3	14.1	12.8	13.4	13.4	12.7	9.9
97	33.9	39.4	30.1	27.8	26.9	28.4	17.0	18.3	19.2	17.6	16.5	16.2
100	32.1	24.6	21.4	21.7	20.8	18.3	19.1	16.8	19.5	23.3	18.8	17.8
101	34.4	30.3	35.8	35.0	22.9	17.9	21.9	19.8	15.5	15.3	16.9	14.3
102	52.9	38.8	32.8	30.6	24.2	25.4	22.1	19.7	21.1	18.5	17.3	16.8

TABLE 3

NYSTAGMIC OUTPUT IN MILLIVOLTS FOR EACH TRIAL AND EACH CAT IN THE CONTROL GROUP

Cat Number	TRIAL											
	1	2	3	4	5	6	7	8	9	10	11	12
86	4.7	3.6	2.2	2.8	2.2	2.0	2.2	1.6	2.0	1.4	1.1	1.4
88	19.0	7.4	11.6	4.1	1.4	2.2	1.0	7.5	4.4	3.6	4.6	3.4
89	33.4	32.7	30.3	21.0	14.4	15.3	11.8	11.3	10.6	9.6	8.6	7.4
91	40.1	28.3	27.8	22.6	11.4	16.3	15.4	9.8	6.4	8.2	8.9	11.4
93	16.2	17.5	23.0	12.3	12.8	10.3	10.8	13.8	9.5	10.7	17.8	7.6
94	24.3	19.6	19.0	13.7	4.7	30.5	20.5	21.1	17.9	12.2	7.5	9.1
96	24.1	20.7	16.6	14.3	11.5	13.2	11.0	12.9	7.4	7.4	7.2	11.7
98	10.8	21.3	9.6	7.8	6.9	8.2	8.1	7.8	10.2	9.6	3.2	9.1
103	10.7	7.2	9.1	6.6	6.3	3.8	6.5	5.6	5.0	5.8	4.9	7.0
104	22.1	11.0	10.8	9.3	8.0	5.6	6.8	5.4	5.0	6.6	7.6	4.6

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FOR ERRATA

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US ARMY MEDICAL RESEARCH LABORATORY
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ERRATA

Report No. 488

HABITUATION OF VESTIBULAR NYSTAGMUS IN THE CAT DURING SUSTAINED AROUSAL PRODUCED BY d-AMPHETAMINE

By Major George H. Crampton, MSC

18 August 1961

Page 4, 7th line from bottom, should read: The difference between the groups was found to be significant at the .01 level.

Page 7, Footnote *, Table 1, should read: .01 level of significance.

Issued 26 Feb 1962

END CHANGE PAGES

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Report No. 488, 18 Aug 61, 11 pp & 11 - 3 illus - 3 tables - Append - Project No. 6X95-25-001, Unclassified Report
The habituation of nystagmus in total darkness was examined for two groups of cats. One group, maintained in a continuous state of high arousal with d-amphetamine sulfate, was compared to a second group of untreated controls. The drug group displayed a nystagmic output nearly 60% greater than that of the control group but showed the same magnitude of habituation. The data of this experiment confirm earlier observations indicating that a reduction of arousal is only one variable responsible for a reduction of nystagmus with repeated testing. Other possible responsible factors are discussed.

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